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# Analysis of common trends in the feeding habits of main demersal fish species on the Flemish Cap

by

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## Abstract

This study describes the diet of core fish species in the Flemish Cap marine community, with emphasis in the changes observed between 1993 and 2008. The analysis was based on trophic species rather than biological ones; trophic species were defined within biological species on the base of diet homogeneity and fish size. Trophic species were divided into four trophic guilds; these guilds were characterized as benthic-pelagic invertebrate, benthic invertebrate, pelagic invertebrate, piscivorous feeders. The multi-year diet matrix for all trophic species was summarized using non-metric multidimensional scaling (MDS). The resulting 3D MDS plot representing the distribution of predators over time in trophic space provided the basic information for the study of common patterns in the diet within the trophic guilds. The MDS scores for each one of the first 3 MDS axes were use to describe the trajectories of the trophic species over time. These trajectories were analyzes using Dynamic factor analysis (DFA); these analyses also included proxy variables representing intra-guild competition, prey availability, and environmental drivers. Results indicate that diet overlap among species has increased in recent years as a consequence of generalized trends towards increasing shrimp and redfish consumption, as well as decreasing consumption of Hyperiidea, Ophiuroidea, Copepoda and Ctenophora. These changes in feeding habits appear to be related to changes in ecosystem availability of prey as well as variations in bottom temperature.

## Introduction

Trophic interactions are among the core issues to be considered during the development and implementation of ecosystem approaches to fisheries management (García et al. 2003, García and Cochrane 2005, Cury et al. 2008). These interactions define the dynamic properties of food webs, and hence, are relevant to understand ecosystem responses to exploitation (e.g. Lilly et al. 2000, Worm and Myers 2003, Frank 2005). In this context, achieving long-term sustainability requires understanding inter-specific interactions, and identifying main trophic pathways.

During their ontogeny, fishes commonly undergo large changes in size which routinely span over 3 to 4 orders of magnitude. These size changes are typically accompanied by important shifts in diet, and often involve a broadening of the prey spectrum with predator size (Gerking 1994, Scharf 2000). For this reason, instead of just describing diets at the level of biological species, the study of food habits in fishes often benefits from considering trophic species (Cohen and Bryan 1984). This type of considerations also allows for a better understanding of energy flows and pathways; a single biological species can be divided into two or more trophic species which can play different functional roles in the food web.

Similarity in the use of food resources (i.e. comparable diets) across trophic species can provide the basis for defining trophic guilds (Simberloff 1991); interaction strength and diet overlap are expected to be stronger among members of the same guild (Pianka 1980). Consequently, if trophic species from the same biological one belong to different guilds, intraspecific resource overlap could be lower than interspecific overlap (Garrison and Link 2000).

Prey availability, competition for food resources, and water temperature are some of the factors expected to influence diet composition in fishes (Wooton 1998, Walters 1993). Marine fish species are characterized by a high degree of opportunistic omnivory or trophic adaptability (Gerking 1994), which can act as stabilizing forces on prey populations; fish predators target the most abundant prey until their relative availability to other suitable prey are reduced (Bax 1998, Gerking 1994). Hence, fish diet composition is largely a reflection of the relative abundances of their prey (Overholtz et al. 2000, Fogarty et al. 1991), These processes are expected to generate common patterns in feeding habits, and hence high overlap in the diets, of fishes as they respond to changes in prey abundance. This leads to a high degree of connectivity in marine food webs (Link 2002), such as that observed in the piscivorous community of Georges Bank (Link et al. 2002, Overholtz et al. 2000, Link and Garrison 2002).

The demersal fish community in the Flemish Cap (NAFO Division 3M, Figure 1), like other ecosystems in the Northwest Atlantic (Link and Garrison 2002, Koen-Alonso et al. 2010) experienced significant changes during the last 30 years (Pérez-Rodriguez et al. 2012). In the mid 1990s, while Atlantic cod *Gadus morhua* collapsed, Northern shrimp *Pandalus boralis* exhibited an unprecedented increase. Some years later, in the early 2000s, Acadian and golden redfish (*Sebastes fasciatus* and *Sebastes marinus*) experienced extreme increases due to very successful recruitment events. This positive trend in redfish started to reverse in 2005, coincident with the beginning of the recovery of Atlantic cod in this system.

From all 65 demersal fish species recorded in EU surveys in the Flemish Cap during 1988 and 2008, more than 99% of the total biomass estimated from these surveys was encompassed by less than 20 fish species (Pérez-Rodríguez et al. 2012). The most dominant in biomass were Atlantic cod, redfishes (beaked redfish *Sebastes mentella*, Acadian redfish and golden redfish), American plaice *Hippoglossoides platessoides*, and Greenland halibut *Reinhardtius hippoglossoides*. Other species with lesser biomass were wolffishes (Atlantic wolffish *Anarhichas lupus*, spotted wolffish *Anarhichas minor*, and Northern wolffish *Anarhichas denticulatus*), thorny skate *Amblyraja radiata*, witch flounder *Glyptocephalus cynnoglossus*, roughead and roundnose grenadier (*Macrourus berglax* and *Nezumia bairdi* respectively) and arctic eelpout *Lycodes reticulatus.*

The food habits of many of these species in the Flemish Cap have been studied in the past (Albikovskaya et al. 1988, Rodríguez-Marín 1994, Torres et al. 2000, Román et al. 2004), as well as some predator-prey size relationships (Lilly 1980), seasonal diet changes (Konstantinov et al. 1985, Albikovskaya and Gerasimova 1993), and the effects of predation on the fish community (Lilly 1985, Lilly and Evans 1986). However, given the significant changes observed in this ecosystem in recent years, an updated description of food habits and theirs changes over time is needed.

Therefore, the objectives of this study are to update and compare the diets of main demersal fish species in the Flemish Cap in the 1993-2008 period, to look for common trends over time, and to explore potential drivers for these trends.

## Material and Methods

### *Stomach content sampling, processing, and basic indices*

Stomach content data from 15 of the most important fish species in biomass in the Flemish Cap were analyzed (Table 1). Stomachs were collected during the EU Flemish Cap surveys in the period 1993-2008. These surveys take place every July, and the stomachs considered in this study were collected up to a depth of 730m (first 19 strata in this survey, see Figure 1) (Pérez-Rodriguez et al. 2012). Arctic eelpout, longfin hake, and roundnose grenadier samples were only available up to 2004. Juvenile individuals of *Sebastes* spp. (<15 cm length) were sampled and treated separately due to the impossibility of discriminating species at this stage. Fish lengths were measured to the nearest cm. Total and individual prey type volumes in each stomach were measured in $cm^3$ using a custom-made "trophometer" (Olaso-Toca 1990).

For each predator species, diets were summarized using two basic indices, the percent volume of a given prey over total volume of stomach contents (*PTV*), and standardized prey volume (*SPV*). These indices were calculated as:

$$PTV_i = \frac{\sum_{k=1}^{n} v_{ik}}{\sum_{i=1}^{I}\sum_{k=1}^{n} v_{ik}} \cdot 100$$

where $PTV_i$ is the percentage in volume of prey $i$; $I$ is the total number of prey categories; $k$ indicates the individual predator, $n$ indicates the total number of predators included in the group for which $PTV$ is being calculated; $v_{ik}$ is the volume of prey $i$ in the stomach of the individual predator $k$.

$SPV$ was calculated as:

$$SPV_{it} = \frac{\bar{v}_{it}}{\sum_{t=1}^{T}\sum_{i=1}^{I} \bar{v}_{it}}$$

where $SPV_{it}$ is the standardized prey volume for prey $i$ in year $t$, where $I$ and $T$ correspond to the total number of prey categories and the total number of years respectively; and $\bar{v}_{it}$ is the average volume for prey $i$ in year $t$.

$PTV$ provides a simple and straightforward way to describe and compare diet composition, while $SPV$ contains information on both diet composition and relative magnitude of the individual consumptions, making it well suited to study overall diet trends.

***Determination of trophic species***

A trophic species has been defined as "a group of organisms with identical sets of prey and identical sets of predators" (Cohen and Briand 1984). In line with this general idea, and considering the ontogenetic diet changes experienced by most fish species, we defined trophic species as size-based subgroups within biological species which show a relatively homogenous diet composition.

For each predator species, changes in diet composition by size were explored by pooling data from all years and calculating *PTV*s by size classes. Those prey species/groups which consistently represented less than 5% in volume were grouped into aggregate prey categories. The resulting matrix of diet composition by size classes was analyzed using chronological clustering (Lengendre et al. 1985) to identify size thresholds in diet composition. These size thresholds were then used to define trophic species, unless the resulting groups were of very low sample size (less than 5 individual fish in a given year); in those cases adjacent groups were merged until all resulting trophic species had sample sizes larger than 5 fishes for all years. Annual cumulative curves of number of prey categories as a function of sample size were used to verify if the sample sizes were adequate.

***Reduction of dimensionality of the diet matrix, and definition of trophic guilds***

The term "diet matrix" often refers to a rectangular matrix defined by predators (e.g. in rows) and prey (e.g. in columns), and where the cells typically contain some index of the presence and/or importance of a particular prey for a particular predator. This "diet matrix" format can be expanded to also describe changes in diet over time by representing in each row the diet of a trophic species in a particular year. In this study, we used such an expanded version of a diet matrix to summarize the changes in the diets of trophic species over time using the $SPV$ index.

Although this expanded diet matrix contains the complete $SPV$ information, its very structure and size makes it difficult to identify patterns in the data. Detection of patterns in food habits would be facilitated by a synoptic, lower-dimensional view of this database. Hence, we used the expanded diet matrix of *SPV*s and the Bray-Curtis index to generate a similarity matrix for "trophic species-year" pairs, which was then used to conduct a non-metric multidimensional scaling (MDS) analysis. This MDS provided a lower-dimensional representation of the similarities in food habits across trophic species and over time.

The diet similarity matrix of "trophic species-year" pairs was also used to identify trophic guilds. A guild is defined as a "group of species that exploit the same kind of ecological resources in a similar way" (Root 1967, Yodzis 1982). We used agglomerative cluster analysis with average linkage on the similarity matrix to provide an initial step towards defining trophic guilds. Results from the cluster analysis, together with ancillary information on general diet patterns and the characteristics of the predators, were integrated to produce the final assignation of trophic species into trophic guilds.

***Analysis of common trends in food habits***

The existence of common trends in food habits among trophic species, and their associations with potential explanatory variables were explored using dynamic factor analysis (DFA) (Zuur et al. 2003).

In DFA, the length of the time series imposes limitations on the number of groups than can be compared within a single analysis (Zuur et al. 2003). These constraints meant that we could not include all trophic species together in a single DFA; we needed to define subsets of trophic species and run separate DFAs for each subset. To do this we used the trophic guilds criteria as a basis for implementing batches of DFAs.

DFA looks for common trends among a set of time series; if we are going to compare diet trajectories across trophic species within a guild we would need a variable that can capture, in a single number, all the diet information for a given trophic species in a given year. Although we were unable to find such a "magical" one-dimensional variable, we can describe the diet evolution over time for a trophic species by describing the trajectory of successive "trophic species-year" points in the "trophic space" generated by the MDS analysis. Consequently, we can study common trends along each one of the MDS axes, by considering the time series defined by the corresponding MDS coordinates for each trophic species. This was the approach taken; we implemented three sets of DFAs for each trophic guild. Each set analyzed the trends associated with one of the three major axes of the MDS trophic space.

In summary, we organized the DFA into batches by trophic guild, and each batch included three different sets of DFAs. These sets considered trends over time along each one of the three major axes in the MDS trophic space, and used the corresponding MDS coordinate value for each "trophic species-year" pair to define the time series to be analyzed.

In addition to exploring common trends, DFA also allows incorporating explanatory variables as drivers for the trajectories (Zuur et al. 2003). In this study, we explored some candidate explanatory variables based on their potential as indicators of important sources of variability in food habits: prey abundance, competition for food, and oceanographic conditions.

Abundance information on different zooplankton groups (Calanoid copepods, Hyperiidea, Chaetognata, and Euphausiacea) from the Continuum Plankton Recorder (CPR) programme (www.sahfos.ac.uk) was used as a proxy for zooplankton prey availability. CPR data series were intended as relative indices of abundance reflecting inter-annual patterns in zooplankton availability. The interpretation and use of CPR data in this context requires caution; CPR data can be highly variable and affected by local conditions, and hence, they are considered more reliable for inter-decadal comparison than for inter-annual ones (Head and Pepin 2010a, 2010b). However, it was still considered here given the lack of better proxies for zooplankton availability. The data used were derived from CPR lines located in the northern vicinity of Flemish Cap, between latitude 47º-53º N and longitude 50º-45º W over the period 1991-2006. The southerly flow of the Labrador Current through the Flemish Pass and northeastern flank of the Flemish Cap transport subarctic zooplankton species downstream from northern regions (Maillet et al. 2005), which justifies the assumption made here that CPR data constitute a plausible proxy for zooplankton in the Flemish Cap. To obtain an average annual value, the geometric mean of average monthly values was estimated to reduce the impact of extreme catches.

Juvenile Sebastes (redfish smaller than 15 cm in length) and Northern shrimp abundances were also employed as proxies for prey abundance. These indices were estimated from EU Flemish Cap survey data for the study area using the standard swept-area method for random stratified sampling designs (Gunderson 1993).

As a proxy for intra-guild competition, the aggregate abundance for the species in the guild was used. The species abundance indices used to construct this explanatory variable were also estimated from EU Flemish Cap survey data for the study area.

The average bottom temperature in July was used as proxy for environmental conditions. These average temperatures were annually estimated from all conductivity, temperature, depth (CTD) stations covered in the EU Flemish Cap survey.

All variables (response and explanatory) used were normalized prior to their use in DFA models. All DFA models within a batch (i.e. associated with a trophic guild) and set (i.e. associated with a MDS axis) were compared, and the best one selected, using the Akaike Information Criterion (AIC) (Burnham and Anderson 2002).

## Results

### *Changes in diet with predator size and determination of trophic species*

A total of 45 prey categories were identified in the diet of the 15 demersal fish species included in this study (Table 2). The examination of the diet composition as a function of predator size indicated that most species exhibit important diet changes as they grow. Only witch flounder and juvenile redfish showed a fairly consistent diet composition across all size classes; to a lesser degree, thorny skate and American place also show a relatively consistent diet with size (Figure 2).

Atlantic cod and Greenland halibut showed a similar diet pattern by size; both predators transition from hyperiids and Northern shrimp, to redfish and other fishes as they increase in size. Atlantic and spotted wolffishes showed a transition from benthic invertebrates and Northern shrimp to a diet dominated more by redfish, while Northern wolffish showed dominance of hyperiids in smaller sizes, comb jellies in middle sizes, and redfish in larger sizes. Longfin hake showed a transition from a mysid dominated diet to a shrimp dominated diet with size, while roughead grenadier showed an invertebrate diet dominated by Northern shrimp at the smaller sizes, transitioning to a diet dominated by jellyfishes and fishes at larger sizes. Arctic eelpout showed an increasing importance of brittle stars in the diet with size, while hyperiids gained more importance in the diet of larger roundnose grenadier. All redfish species above 15 cm length showed a decline in the dominance of copepods and an increase in the presence of Northern shrimp in the diet with size (Figure 2).

After examination of the chronological clustering results[1], the associated sample sizes of the resulting groups, and the necessary merging of groups to maintain acceptable sample sizes, 9 of the 15 original species/groups considered were subdivided into trophic species for subsequent analyses. In all cases these trophic species essentially involved dividing a biological species into small and large size categories (Table 1). Based on the curves of cumulated prey categories as a function of sample size[1], the sample sizes by year for defined trophic species (Table 3) were considered acceptable.

### *Changes in diet over the period 1993-2008*

Important changes in food habits were observed over the study period (Figure 3). Most trophic species exhibited an increase in dominance of Northern shrimp in their diets, especially since the late 1990s. Consequently, other prey showed significant declines in their contribution to the diets. For example, declines were noted in hyperiids in both trophic species of Atlantic cod (GM1 and GM2) and small Greenland halibut (RH1); several benthic invertebrates (especially brittle stars and sea urchins) in small Atlantic (AL1) and spotted (AM1) wolffishes, American plaice (HP) and Arctic eelpout (LR); and pelagic invertebrates (copepods, chaetognats and hyperiids) in all three large redfish trophic species (SF2, SMa2 or SMe2). The increased dominance of shrimp was also observed on species that had always had shrimp as an important prey, like longfin hake (PC) and thorny skate (AR).

On the other hand, large trophic species like Atlantic (AL2) and spotted (AM2) wolfishes, Northern wolfish (AD), Atlantic cod (GM2), and Greenland halibut (RH2) showed an increase of redfish in their diets in the early 2000s; even large golden redfish (SMa2) presented higher cannibalism on congeners since 2006. This increase of redfish meant a decline of combjellies in the diet of Northern wolfish (AD), hyperiids in the diet of large Atlantic cod (GM2), benthic invertebrates and shrimp in the diet of Atlantic (AL2) and spotted (AM2) wolfishes, and a reduction of other fishes in the diet of large Greenland halibut (RH2).

The consumption of pelagic invertebrates by redfishes experienced important variations, especially the decline of copepods in 1995-1996 and 2003-2004, partly due to an increase in other crustaceans and Northern shrimp. Witch flounder (GC) showed very little change in its diet over time, with polychaetes being the main prey over the entire study period.

### *Reduction of dimensionality: trophic space*

The MDS results indicated that a three dimensional representation was adequate to summarize the information contained in the expanded diet matrix (stress=0.15). The distribution of data points in the resulting 3D “trophic space” (Figure 4) provides the basis for understanding how the trophic structure of

[1] These results are only used as an intermediate step in the process of defining the operational species used in this paper. For the sake of brevity they are not provided here, but they are available from the lead author upon request.

the Flemish Cap changed during the study period. In general, trophic species seem to occupy relatively well defined regions in trophic space, although there is significant overlap among many of them (Figure 4). The differences in scattering in trophic space is indicative of the relative stability of diet over time among trophic species; little scatter means little change in the diet, while large scatter indicates substantial change.

This MDS plot can also be used to map prey categories in trophic space by considering the most important prey for each trophic species in each year. This simple approach (it only involves re-labeling each point with the name of the most important prey for that predator group in that year) allows identifying which areas in trophic space are dominated by specific prey groups. This information (Figure 5) is essential to translate the changes in the values along each MDS-axis in terms of actual changes in diet. In this context, the changes in diet along each one of the three MDS axes can be summarized as follows:

- Dimension I (axis 1): This axis shows a general transition in both trophic species and their main prey (Figures 4 and 5). Going from negative to positive values along this axis, most negative values correspond to juvenile redfishes (SJ) feeding on copepods, then small redfishes (SF1, SMa1, SMe1), which are followed by large redfishes (SF2, SMa2, SMe2) feeding on hyperiids. Values nearing zero correspond to trophic species feeding on hyperiids and Northern shrimp. As values become positive, a larger suite of prey appears as important (Northern shrimp, *Sebastes* sp., other fishes, Polychaeta, Bivalvia, Ophiuroidea, and Ctenophores). The highest values along this axis correspond to large wolffishes (AD, AL2 and AM2).
- Dimension II (axis 2): Along this axis, the most negative values correspond to Northern wolfish (AD) with Ctenophora as its exclusive dominant main prey, while the highest positive values correspond to witch flounder (GC) and Polychaeta as its corresponding main prey. The rest of the trophic species are fairly clumped in a small range around zero with Ophiuroidea, hyperiids, Northern shrimp, copepods, and *Sebastes* sp as the dominant prey.
- Dimension III (axis 3): With the exception of the redfish trophic species, Northern wolfish (AD), roundnose grenadier (NB1, NB2), and large Greenland halibut (RH2), trophic species are widely scattered along this dimension. From the most negative to the zero value Northern shrimp is the most common dominant prey in the diet. Around zero other dominant prey like *Sebastes* sp., other fishes, hyperiids, and copepods appear. In the positive range the main prey are hyperiids, copepods, polychaetes and redfish, with juvenile redfish (SJ), large golden redfish (SMa1), roundnose grenadier (NB1, NB2), Atlantic cod (GM1, GM2), witch flounder (GC), and spotted (AM1, AM2) and Atlantic (AL1, AL2) wolfishes being the common trophic species in this region. The highest positive values along this axis correspond to Ophiuroidea and Ctenophora as dominant prey in American plaice (HP) and Northern wolffish (AD) respectively.

*Determination of trophic guilds*

Taxonomic identity of the predators and descriptive diet information, together with the results from agglomerative clustering (Table 4), provided the basis for defining the following trophic guilds:

Trophic guild I (AR, GM1, MB1, MB2, NB1, NB2, PC and RH1). These species were mostly assigned to clusters *g* and *e*. For all these trophic species Northern shrimp was a very important prey, either since early in the study period or later on, when there was a decline in the consumption of hyperiids.

Trophic guild II (AL1, AM1, GC, HP and LR). These trophic species were assigned to several different clusters, but most years were grouped in clusters *g* and *c*, with the exception of witch flounder (GC) which was grouped in cluster *a*. All these trophic species had different benthic invertebrates like Ophiuroidea, Polychaeta, Bivalvia, Asteroidea and Echinoidea as the main prey at the beginning of the time series. In the late 1990s, there was a transition in prey importance from benthic invertebrates to Northern shrimp, even in witch flounder (GC), although in this case there was only a slight increase.

Trophic guild III (SF1, SF2, SJ, SMa1, SMa2, SMe1 and SMe2). This is the redfish trophic guild. Most of these trophic species were grouped in cluster *d*, although large redfishes (SF2, SMa2 and SMe2) had several years assigned to cluster *g*. This group can be characterized by a diet strongly based on pelagic invertebrates (Copepoda, Hyperiidea, Chaetognata, Euphausiacea) with Northern shrimp increasing in importance since the early 2000s.

Trophic guild IV (AD, AL2, AM2, GM2 and RH2). All these trophic species had several years grouped in cluster *f*, with the exception of RH2 (cluster *g*). Although this group showed very heterogeneous feeding habits until late 1990s (reflected in the diversity of clusters during this period: cluster *b* for AD and AM2,

cluster c for AL2 and cluster *e* for GM2), all trophic species experienced an increment in the consumption of *Sebastes* sp. since the early 2000s (corresponding to their grouping in cluster *f*). Even though RH2 was not grouped in cluster *f*, it was assigned to this trophic guild because it showed a highly piscivorous diet, with *Sebastes* sp. increasing in importance since 2000.

*Analysis of common trends in food habits*

Notwithstanding the variability across trophic species, coherent changes in the MDS scores over time appear to exist within each trophic guild (Figure 6). Some key common patterns were:

- Dimension I: in the late 1990s, trophic guild I seemed to present a tendency toward positive values, trophic guild II showed a sharp decline from positive to negative values, and trophic guild IV showed a declining pattern until late 1990s, with the exception of large Atlantic cod (GM2) which presented the opposite trend. Trophic guild III showed a moderate increasing trend in the early 2000s, although it was not so important or stable in the smaller trophic species of this guild.
- Dimension II: Trophic guild I showed a highly variable pattern over time with no apparent trend. Trophic guild II showed a very similar pattern to the one seen in Dimension I. Trophic guild III showed an increasing pattern until the mid 2000s, and trophic guild IV showed a period of increase or decrease (depending on the trophic species) until early 2000s, followed by a relatively stable period.
- Dimension III: In this dimension of trophic space there was a very clear declining pattern, which was very similar across all trophic species of all trophic guilds.

When no explanatory variables were considered, the lowest AICs (Table 5) corresponded to DFA models with only one common trend in all cases (Figure 7). Those trophic species with factor loadings greater than 2 were considered to be influenced significantly by the trend (Tables 6, 7, 8 and 9).

In trophic guild I, small Atlantic cod (GM1) and Greenland halibut (RH1), together with roughead grenadier (MB1, MB2) were the trophic species more influenced by common trends; thorny skate (AR) and small roundnose grenadier (NB1) did not present any common trend with the remaining trophic species in any dimension (Table 6). In trophic guild II, all trends were common to most species (Table 7), and in trophic guild III all species presented at least one common trend with some other species in the guild (Table 8). The results for trophic guild IV showed that these species shared a common trend in all dimensions, mainly Northern (AD), large Atlantic (AL2) and spotted (AM2) wolffishes and large Atlantic cod (GM2) (Table 9).

From the positions of each trophic species in trophic space (Figures 4), and the location of "prey areas" in this space (Figure 5), the obtained common trends globally describe the increase in Northern shrimp consumption since late 1990s, as well as the increase in consumption of redfishes by trophic guild IV. On the other hand, these patterns also reflect the movement away from "prey areas" characterized by the consumption of hyperiids, copepods, ophiurids, ctenophore and others that were the "starting location" in trophic space for many trophic species at the beginning of the study period.

The explanatory variables considered for the DFA showed different signals over time (Figure 8). Water temperature, included as a proxy for environmental conditions, did not show any obvious pattern and had minimum values in the mid 1990s.

The sum of the abundances of the species within a guild was considered a proxy for representing intra-guild competitive effects. The abundance of trophic guild I presented a sharp decline in the early 1990s, while the abundance of trophic guild IV was at its highest in the late 1990s (Figure 8).

In order to define which prey were worth considering as drivers in the DFA models for each trophic guild, Pearson correlation coefficients between the time series of *SPV* for each prey category and the corresponding scores along each one of the MDS axes for each trophic species were calculated. Those prey categories which presented correlations higher than 0.5 for at least 2/3 of the trophic species within a guild and trophic space dimension were included as prey drivers for the corresponding DFA models (Table 10).

Proxies for the availability of hyperiids, copepods, Northern shrimp, and juvenile redfishes were included in the DFA modeling exercise. Northern shrimp showed an important increase in the late 1990s. Redfishes started to increase in 2003 while pelagic invertebrates showed a declining pattern. For other prey categories worthy of consideration (e.g. Ophiuroidea and Polychaeta, see Table 10) there were no

data available that could be used as a proxy for their trends in availability over time, and hence, it was not possible to include them in the DFA modeling exercise.

When explanatory variables were introduced in the models, all trophic guilds, except trophic guild II, showed a reduction in AIC values in comparison with the corresponding model without explanatory variables (Table 5). The best DFA models for all trophic guilds and dimensions contained only one common trend (Table 5); these common trends often presented differences when compared to the common trend obtained in the model without explanatory variables (Figure 7). The variable included in the best models in guilds I, III and IV was intra-guild competition, represented by the total abundance of the trophic species in that guild (Table 5).

The abundance of pelagic invertebrates like Hyperiidea for trophic guild I (Table 6) and Calanidae for trophic guild III (Table 8) emerged as important drivers and were included in their corresponding best models for dimensions I and II (Tables 5, 6 and 8). The abundance of juvenile redfishes was also an important driver for trophic guild IV (Table 9). Overall the most widespread and influential prey was Northern shrimp (Tables 5, 6, 8, and 9).

Bottom temperature was especially important in trophic guild III (in all three dimensions), although it was also included in the model for dimension II in guild IV (Tables 8 and 9).

Although the consideration of explanatory variables clearly improved model fit in most cases (Table 5), common trends, and the related factor loadings for the different species, remained relatively unchanged (Tables 6, 8, and 9). Overall, DFA models provided a reasonable description of the MDS score trajectories for most trophic species and dimensions (Figures 9, 10, 11, and 12).

*Global changes in trophic space*

The location in trophic space by blocks of time was examined by re-labeling the data in the MDS plot according to three blocks of years (1993-1997, 1998-2002 and 2003-2008). In this light, the 3D MDS showed a progressive decrease in the dispersion of trophic species-year data points over time (Figure 13). The estimated variance for each block of years along each dimension supported this observation of shrinking trophic space over time.

**Discussion**

As expected, diet composition showed clear changes with predator size in most fish species. These differences not only support the consideration of trophic species for the study of feeding habits in this fish assemblage, but they were important enough that it often led to assigning trophic species from the same biological species into different trophic guilds.

The trophic guilds identified in this study can be functionally described as: benthic-pelagic invertebrate feeders (Trophic Guild I), characterized by the consumption of Northern shrimp and hyperiids; benthic invertebrate feeders (Trophic Guild II), preying on many different benthic invertebrates, most notably brittle stars (Ophiuroidea); pelagic invertebrate feeders (Trophic Guild III), defined by the consumption of copepods, hyperiids, and chaetognats; and piscivorous feeders (Trophic Guild IV), feeding on many fish species, but with redfish as a dominant prey in the later years. Our results also make clear that the temporal scale considered is key in determining trophic guild membership; as diets change over time, trophic species membership to a guild can also change (e.g. an important element defining the piscivorous feeders as a single guild is the shared importance of redfish in the diet, which was only observed in the later part of the study period).

Previous studies of the Flemish Cap reported feeding habits in the 1970s and 1980s similar to the ones observed here during the early and mid 1990s. Most of these analyses were focused on Atlantic cod, American plaice, redfish and Greenland halibut (Konstantinov et al. 1985, Paz et al. 1989, Paz & Casas 1996); others were focused on the three wolffishes (Albikovskaya 1983, Templeman 1985, Nelson & Ross 1992). Since the late 1990s important changes in feeding habits have occurred, most notably an increase in shrimp consumption; this is consistent with observations in other areas in the North Atlantic (Parsons 2005, Link and Idoine 2009). Several common trends were associated with an increase in shrimp consumption over time (mainly along dimension III); this phenomenon was reflected in the reduction of the variance in trophic space, and could be seen as an indication of generalized omnivory and opportunism in fishes. Another important common trend was the increase in consumption of redfishes in piscivorous feeders (trophic guild IV) since 2003.

Common patterns in feeding habits across different fish species are often the response to changes in the abundance of some important prey, environmental conditions, and/or fish community dynamics (Link et al. 2002, Overholtz et al. 2000, Link and Garrison 2002, Feyrer et al. 2003). In our study, intra-guild

competition, prey availability, and environmental conditions were also identified as important drivers for the changes in diet over time (Table 5). Only in the case of benthic feeders (trophic guild II) did the inclusion of explanatory variables not improve model fit. The fact that there was no abundance data for benthic invertebrates, especially brittle stars, could likely be the reason behind this result.

In many cases, those prey categories initially identified as important based on diet composition were the ones for which their inclusion in the DFA led to models with the lowest AICs. This observation could suggest that indices of abundance for those prey species may be useful indicators of the trends in diet for a given trophic guild. However, the associated coefficients to these explanatory variables were statistically significant only in some cases (Tables 6, 8, and 9). Furthermore, the sign of the coefficients often did not agree with *a priori* expectations based on a) diet composition, and b) how those prey categories load onto the MDS axes. It is intriguing that hypotheses about which species would be expected to improve model fit were often supported by the results, while the details of how those improvements should operate within the model (i.e. sign of coefficients) were seldom supported.

In principle, these observations reinforce the idea that the linkage between diet composition and prey availability cannot be expected to follow simple linear relationships; interactions among the relative availability of alternative prey can certainly affect how expectations on coefficient signs in this kind of model should be constructed. It is also possible that the reduction in dimensionality of the extended trophic matrix (which, even though works well, is certainly not distortion free) makes it impossible to securely predict what the expected signs should be. In any case, the examination of these apparent contradictions warrants further examination.

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**Table 1**. Fish species considered in the present study, with indication of which ones were divided into trophic species. *Fish size* indicates length in cm used as a threshold to define small and large size categories that were defined as trophic species; "All" indicates those biological species for which all sizes were included into a single trophic species. *Trophic species* indicates the abbreviations used throughout the text to refer to the trophic species; where appropriate, small and large size categories are indicated in the trophic species abbreviation by the numerals 1 and 2 respectively.

| *Biological species* | *Fish size* | *Trophic species* |
|---|---|---|
| Thorny skate *Amblyraja radiata* | All | AR |
| Northern wolffish *Anarhichas denticulatus* | All | AD |
| Atlantic wolffish *Anarhichas lupus* | 41 | AL1; AL2 |
| Spotted wolffish *Anarhichas minor* | 46 | AM1; AM2 |
| Atlantic Cod *Gadus morhua* | 46 | GM1; GM2 |
| Greenland halibut *Reinhardtius hippoglossoides* | 31 | RH1; RH2 |
| American plaice *Hippoglossoides platessoides* | All | HP |
| Witch flounder *Glyptocephalus cynnoglossus* | All | GC |
| Arctic eelpout *Lycodes reticulatus* | All | LR |
| Longfin hake *Phycis chesteri* | All | PC |
| Roughead grenadier *Macrourus berglax* | 15.5 | MB1; MB2 |
| Roundnose grenadier *Nezumia bairdi* | 6 | NB1, NB2 |
| Juvenile redfishes (all redfishes ) *Sebastes* spp | All | SJ |
| Acadian redfish *Sebastes fasciatus* | 21.5 | SF1; SF2 |
| Golden redfish *Sebastes marinus* | 27.5 | SMa1; SMa2 |
| Beaked redfish *Sebastes mentella* | 27.5 | SMe1; SMe2 |

**Table 2**. Prey categories used in this study. Some prey categories include only one taxon, while others aggregate many taxa. Aggregate categories were based on both consideration of the importance in the diet of the constituent species, as well as ability to identify prey items to the lowest taxonomic level.

| Prey category | Prey species included |
|---|---|
| *Anarhichas* sp. | *Anarhichas denticulatus*; *Anarhichas lupus*; *Anarhichas minor*; *Anarhichas* sp. |
| Asteroidea | Asteroidea |
| *Bentheuphausia amblyops* | *Bentheuphausia amblyops* |
| Bivalvia | Bivalvia |
| Chaetognata | Chaetognata |
| *Chauliodus sloani* | *Chauliodus sloani* |
| *Chionoecetes opilio* | *Chionoecetes opilio* |
| Copepoda | Calanoida; Copepoda |
| Unidentified Crustaceans | Brachyura; Crustacea; Decapoda Crustacea; Natantia |
| Ctenophora | Ctenophora |
| Echinoidea | Echinoidea |
| *Erythrops* sp | *Erythrops* sp |
| Euphausiacea | Euphausiacea |
| *Gadus morhua* | *Gadus morhua* |
| Gammaridea | Gammaridea |
| Hyperiidea | Hyperiidea |
| *Illex coindetii* | *Illex coindetii* |
| *Lampadena speculigera* | *Lampadena speculigera* |
| *Lebbeus polaris* | *Lebbeus polaris* |
| *Lithodes maja* | *Lithodes maja* |
| *Lumpenus lumpretaeformis* | *Lumpenus lumpretaeformis* |
| *Lycodes* sp | *Lycodes esmarki*; *Lycodes Polaris*; *Lycodes reticulates*; *Lycodes* sp |
| *Macrourus berglax* | *Macrourus berglax* |
| *Magnisudis atlantica* | *Magnisudis atlantica* |
| *Malacosteus niger* | *Malacosteus niger* |
| *Meganyctiphanes norvegica* | *Meganyctiphanes norvegica* |
| Unidentified Molluscs | Cephalopoda; Decapoda; Mollusca; Oegopsida; Teuthidae |
| Myctophidae | Myctophidae; *Myctophum punctatum* |
| Mysidacea | Mysidacea |
| *Notolepis risso* | *Notolepis risso* |
| Ophiuroidea | Ophiuroidea |
| *Pandalus borealis* | *Pandalus borealis* |
| Polychaeta | Polychaeta; *Polychaeta errantia*; *Polychaeta sedentaria* |
| Scyphozoa | Scyphozoa |
| *Sebastes* sp | *Sebastes marinus*; *Sebastes mentella*; *Sebastes* sp |
| *Sergestes arcticus* | *Sergestes arcticus* |
| *Serrivomer beani* | *Serrivomer beani* |
| Sipunculida | Sipunculida |
| *Spirontocaris lilljeborgii* | *Spirontocaris lilljeborgii* |
| Unidentified Fishes | Pisces |
| Other artropods | *Acanthephyra pelagica*; *Acanthephyra purpurea*; *Acanthephyra* sp; *Ammotrypane aulogaster*; Amphipoda; *Argis dentata*; Caprellidae; Caridea; Crangonidae; Cumacea; *Eucopia grimaldii*; Galatheidae; *Gennadas elegans*; *Gennadas* sp; *Gnatophausia* sp; *Hyas coarctatus*; *Hyas* sp; Isopoda; *Oplophorus spinosus*; Ostracoda; Paguridae; *Pandalus montagui*; *Parapasiphaea sulcatifrons*; *Pasiphaea tarda*; Pasiphaeidae; Penaeidea; Polynoidae; *Pontophilus norvegicus*; *Pseudomma* sp; Pycnogonidae; *Rhachotropis aculeata*; *Sabinea hystrix*; *Sabinea sarsi*; *Sclerocrangon ferox*; *Sergia robusta*; Serpulimorpha; *Spirontocaris* sp; *Thysanoessa longicaudata*; *Tole spinosa* |
| Other invertebrates | Anthozoa; Aphroditidae; Ascidiacea; Brachiopoda; Bryozoa<br>Cnidaria; Crinoidea; Undetermined Echinoidea; Echinodermata; Holothurioidea; Nematoda; Poriphera; Priapulido; Siphonophora; Thaliacea; Thecaphora |
| Other molluscs | *Bathypolypus arcticus*; *Bathypolypus* sp; *Brachioteuthis* sp; Gasteropoda; *Gonatus* sp; *Histioteuthis reversa*; *Histioteuthis* sp; *Illex illecebrosus*; Nudibranchia; Octopoda; *Onichotheuthys banksii*; Opisthobranquia; Pectinidae; Scaphopoda; *Semirossia* sp; Sepiida; Sepiolidae |
| Other fishes | *Alepocephalus* sp; *Amblyraja hyperborea*; *Amblyraja radiata*; *Ammodytes dubbius*; *Ammodytes* sp; Anguilliformes; *Antimora rostrata*; *Argentina* sp.; *Argyropelecus hemigymnus*; *Argyropelecus* sp; *Aspidophoroides monopterygius*; *Bathylagus euryops*; *Benthosema glaciale*; *Borostomias antarcticus*; *Brotulotaenia brevicauda*; Ceratoideoa; *Ceratoscopelus maderensis*; *Chiasmodon niger*; *Coryphaenoides rupestris*; *Cottunculus microps*; *Cottunculus* sp; *Cyclothone microdon*; *Cyclothone* sp; *Enchelyopus cimbrius*; Gadidae; *Gaidropsarus ensis*; *Gaidropsarus* sp; Gonostomatidae; *Hippoglossoides platessoides*; *Leptagonus* (*agonus*) *decagonus*; *Leptoclinus maculates*; Liparidae; *Liparis* sp; *Lycodes vahlii*; Macrouridae; *Mallotus villosus*; *Maurolicus muelleri*; *Nemichthys scolopaceus*; *Nezumia bairdii*; *Normichthys operosus*; *Notoscopelus* sp; Paralepididae; *Phycis chesteri*; Pleuronectiformes; *Poromitra megalops*; *Poromitra* sp; *Protomictophum arcticum*; *Pseudoscopelus scriptus*; Rajidae; *Reinhardtius hippoglossoides*; Saccopharyngidae; *Scomberesox saurius*; *Scopelogadus beanie*; *Stomias boa*; *Synaphobranchus kaupi*; *Triglops murrayi*; *Tryglops* sp; *Urophycis* sp |
| Miscellaneous | algae; eggs; larvae; rocks; placophora; bird remains; Fishing processing remains |

**Table 3**. Number of sampled individuals by trophic species and year. Empty cells indicate no samples in that particular year.

| Trophic species | Year | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2008 |
| AD | | 15 | 26 | 30 | 24 | 25 | 12 | 31 | 28 | 46 | 30 | 49 | 21 | 50 | 45 |
| AL1 | 71 | 43 | 157 | 103 | 97 | 131 | 106 | 104 | 86 | 142 | 109 | 152 | 183 | 110 | 46 |
| AL2 | 70 | 46 | 77 | 38 | 37 | 35 | 30 | 29 | 24 | 49 | 29 | 62 | 29 | 56 | 51 |
| AM1 | 25 | 50 | 85 | 64 | 61 | 49 | 20 | 29 | 10 | 18 | 37 | 125 | 53 | 76 | 25 |
| AM2 | 56 | 49 | 102 | 56 | 70 | 58 | 57 | 35 | 26 | 54 | 25 | 51 | 29 | 53 | 46 |
| AR | 126 | 59 | 70 | 51 | 58 | 62 | 59 | 90 | 103 | 81 | 336 | 239 | 134 | 157 | 225 |
| GC | 178 | 108 | 99 | 73 | 35 | 34 | 83 | 83 | 163 | 52 | 130 | 143 | 53 | 56 | 208 |
| GM1 | 653 | 415 | 337 | 272 | 222 | 24 | 28 | 57 | 289 | 131 | 66 | 237 | 133 | 359 | 329 |
| GM2 | 220 | 144 | 146 | 160 | 213 | 144 | 147 | 177 | 72 | 92 | 71 | 170 | 223 | 266 | 450 |
| HP | 338 | 323 | 263 | 193 | 137 | 126 | 214 | 172 | 229 | 135 | 95 | 470 | 118 | 132 | 220 |
| LR | 72 | 77 | 141 | 131 | 99 | 84 | 78 | 89 | 78 | 155 | 70 | 46 | | | |
| MB1 | 20 | 24 | 35 | 47 | 55 | 78 | 62 | 56 | 150 | 64 | 277 | 45 | 115 | 49 | 35 |
| MB2 | 65 | 23 | 41 | 63 | 44 | 67 | 58 | 87 | 107 | 84 | 93 | 39 | 80 | 80 | 66 |
| NB1 | 76 | 83 | 121 | 43 | 52 | 62 | 106 | 79 | 87 | 123 | 140 | 66 | | | |
| NB2 | 51 | 64 | 35 | 88 | 91 | 59 | 88 | 55 | 86 | 78 | 85 | 16 | | | |
| PC | 46 | 57 | 31 | 45 | 23 | 115 | 78 | 115 | 78 | 56 | 159 | 102 | | | |
| RH1 | 166 | 78 | 297 | 273 | 221 | 181 | 123 | 95 | 218 | 235 | 218 | 356 | 81 | 93 | 41 |
| RH2 | 225 | 232 | 371 | 357 | 426 | 437 | 622 | 414 | 502 | 434 | 371 | 182 | 215 | 135 | 37 |
| SF1 | 32 | 109 | 213 | 150 | 193 | 163 | 152 | 179 | 251 | 344 | 256 | 194 | 115 | 206 | 138 |
| SF2 | 77 | 64 | 78 | 91 | 89 | 81 | 91 | 130 | 169 | 186 | 125 | 125 | 65 | 75 | 123 |
| SJ | 88 | 71 | 41 | 57 | 90 | 92 | 78 | 129 | 338 | 368 | 300 | 138 | 99 | 110 | 157 |
| SMa1 | 73 | 94 | 207 | 173 | 163 | 150 | 93 | 66 | 109 | 148 | 166 | 257 | 143 | 210 | 195 |
| SMa2 | 69 | 51 | 50 | 63 | 115 | 66 | 85 | 163 | 170 | 124 | 86 | 82 | 14 | 53 | 146 |
| SMe1 | 82 | 91 | 367 | 194 | 297 | 200 | 236 | 185 | 343 | 357 | 234 | 316 | 122 | 243 | 131 |
| SMe2 | 79 | 122 | 131 | 81 | 83 | 54 | 53 | 98 | 107 | 165 | 47 | 87 | 76 | 71 | 64 |

**Table 4**. Tabulated results from the agglomerative cluster analysis (with average linkage), and assignation of trophic species to trophic guilds. At a 30% similarity level, the analysis distinguished 7 clusters (labeled as clusters a-g); this table indicates the number of "trophic species-year" data points that were grouped in each cluster, discriminated by trophic species. These results were used, together with information on diet patterns, to assign each trophic species to a trophic guild; the final trophic guild designation is indicated in the right-most column.

| Trophic species | Number of "trophic species-year" included in each cluster | | | | | | | Trophic guild assignation |
|---|---|---|---|---|---|---|---|---|
| | Cluster a | Cluster b | Cluster c | Cluster d | Cluster e | Cluster f | Cluster g | |
| AR | | | | | | | 15 | 1 |
| GM1 | | | | | 9 | | 6 | 1 |
| MB1 | | | 3 | | | | 12 | 1 |
| MB2 | | | | | | | 15 | 1 |
| NB1 | | | | | 12 | | | 1 |
| NB2 | | | | | 11 | | 1 | 1 |
| PC | | | | 1 | | | 11 | 1 |
| RH1 | | | | | 5 | | 10 | 1 |
| AL1 | | | 9 | | | | 6 | 2 |
| AM1 | | 2 | 3 | | 1 | 3 | 6 | 2 |
| GC | 15 | | | | | | | 2 |
| HP | | 1 | 8 | | 3 | | 3 | 2 |
| LR | 1 | | 5 | | | | 6 | 2 |
| SF1 | | | | 15 | | | | 3 |
| SF2 | | | | 13 | | | 2 | 3 |
| SJ | | | | 15 | | | | 3 |
| SMa1 | | | | 15 | | | | 3 |
| SMa2 | | | | 10 | | 2 | 3 | 3 |
| SMe1 | | | | 14 | 1 | | | 3 |
| SMe2 | | | | 3 | | | 12 | 3 |
| AD | | 10 | | | | 4 | | 4 |
| AL2 | | | 5 | | | 8 | 2 | 4 |
| AM2 | | 4 | | | | 11 | | 4 |
| GM2 | | | | | 6 | 7 | 2 | 4 |
| RH2 | | | | | | | 15 | 4 |

**Table 5**.The AIC for DFA models with only one trend and models with one trend and explanatory variables for each trophic guild and dimension. The selected models are also presented, which included explanatory variables in all cases except trophic guild II.

| Trophic guild | Dimension | AIC Only Com.trend | AIC Com.Trend + Expl.Var. | Selected model |
|---|---|---|---|---|
| I | I | 339 | 262.4 | 1 trend+SumGroupI+Northern shrimp+Hyperiidea |
| I | II | 342.5 | 243.8 | 1 trend+SumGroupI+Northern shrimp+Hyperiidea |
| I | III | 293.1 | 244.6 | 1 trend+SumGroupI+Northern shrimp +SumGroupIII |
| II | I | 208.1 | | 1 trend |
| II | II | 205.5 | | 1 trend |
| II | III | 195.2 | | 1 trend |
| III | I | 282.5 | 276.6 | 1 trend+BottomTemp+SumGroupIII+Calanidae |
| III | II | 292.6 | 277.3 | 1 trend+BottomTemp+ SumGroupIII +Calanidae |
| III | III | 330.9 | 311.7 | 1trend+BottomTemp+Northern shrimp+Calanidae+Hyperiidea |
| IV | I | 216 | 207.8 | 1 trend+SumGroupIV |
| IV | II | 209.1 | 196.4 | 1trend+ BottomTemp+Northern shrimp +Juvenile*Sebastes* |
| IV | III | 212.4 | 200.1 | 1 trend+Northern shrimp |

SumGroupI, SumGroupIII and SumGroupIV: sum of abundance (from the EU surveys) of species from trophic guilds I, III and IV respectively.
BottomTemp: bottom water temperature
Juvenile*Sebastes*: abundance (from the EU surveys) of juvenile redfish smaller than 15 cm.
Calanidae, Hyperiidea, Northern shrimp: Biomass indexes from the CPR database (for Calanidae and Hyperiidea) and EU surveys (Northern shrimp).

**Table 6**. Estimated factor loadings for common trends in the DFA models with no explanatory variables, as well as factor loadings and regression parameters (with their respective p-values: *<0.05; **<0.01; +++<0.001) in models also with explanatory variables for the three dimensions of trophic space in trophic guild I. Factor loadings higher than 0.2 are presented in bold font.

| | | DFA without explanatory variables | DFA with explanatory variables | | | | |
|---|---|---|---|---|---|---|---|
| Trophic Guild I | | Trend | Trend | Coefficients (significance) | | | |
| Dimension | Trophic species | Factor Loadings | Factor Loadings | Hyperiidea | Sum Group III | Northern shrimp | Sum Group1 |
| I | AR | -0.172 | 0.154 | 0.995** | | 0.472*** | 0.392*** |
| I | GM1 | **0.222** | **0.27** | 0.131 | | 0.143 | 0.132 |
| I | MB1 | 0.042 | -0.002 | 0.188 | | 0.078 | -0.591** |
| I | MB2 | **-0.253** | 0.108 | 0.233 | | 0.32 | 0.638** |
| I | NB1 | -0.002 | -0.146 | -0.579*** | | -0.227 | -0.147 |
| I | NB2 | -0.072 | 0.081 | -0.292 | | -0.619** | 0.09 |
| I | PC | 0.159 | 0.13 | 0.081 | | -0.043 | -0.321 |
| I | RH1 | **0.386** | **0.275** | 0.603*** | | 0.442*** | -0.159 |
| II | AR | -0.121 | **0.274** | -1.226* | | -0.803** | -0.394*** |
| II | GM1 | -0.13 | 0.006 | -0.228 | | -0.292 | -0.283 |
| II | MB1 | **0.3** | 0.118 | -0.235 | | -0.346*** | 0.641* |
| II | MB2 | **0.269** | 0.154 | -0.231 | | -0.402 | 0.074 |
| II | NB1 | 0.033 | 0.038 | -0.201 | | 0.085 | 0.365 |
| II | NB2 | **0.236** | 0.02 | 0.088 | | -0.238 | 0.466*** |
| II | PC | -0.024 | **-0.481** | 0.613 | | 0.35 | 0.394 |
| II | RH1 | **-0.116** | **-0.216** | 0.176 | | 0.264 | 0.353 |
| III | AR | 0.063 | -0.174 | | 0.215* | -0.359 | 0.079 |
| III | GM1 | **0.204** | **0.239** | | 0.224 | 0.081 | -0.035 |
| III | MB1 | **0.222** | -0.104 | | 0.142* | -0.507** | 0.622* |
| III | MB2 | 0.113 | -0.055 | | 0.215** | 0.048 | 0.146 |
| III | NB1 | 0.046 | -0.059 | | 0.523** | -0.412*** | -0.044 |
| III | NB2 | 0.006 | 0.103 | | 0.214* | 0.179 | -0.356*** |
| III | PC | **0.207** | 0.071 | | 0.423 | 0.276 | 0.428*** |
| III | RH1 | **0.265** | 0.085 | | 0.171*** | -0.405*** | 0.119 |

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**Table 7**. Factor loadings in the DFA model with no explanatory variables for trophic guild II in the three dimensions of trophic space.

| Trophic species | Dimension I | Dimension II | Dimension III |
|---|---|---|---|
| AL1 | **0.556** | **0.342** | **0.360** |
| AM1 | **0.460** | **0.334** | 0.178 |
| GC | 0.093 | 0.139 | **0.331** |
| HP | **0.350** | **0.491** | **0.346** |
| LR | **0.450** | 0.116 | **0.263** |

**Table 8**. Estimated factor loadings for common trends in the DFA models with no explanatory variables, as well as factor loadings and regression parameters (with their respective p-values: *<0.05; **<0.01; +++<0.001) in models also with explanatory variables for the three dimensions of trophic space in trophic guild III. Factor loadings higher than 0.2 are presented in bold font.

| Trophic guild III | | DFA without explanatory variables | DFA with explanatory variables | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | Trend | Trend | Coefficients (significance) | | | | |
| Dimension I | Trophic species | Factor Loadings | Factor Loadings | Hyperiidea | Sum Group III | Northern shrimp | Bottom Temp | Calanidae |
| I | SF1 | **0.221** | 0.137 | | 0.656*** | | -0.459 | 0.019 |
| I | SF2 | **0.26** | **0.202** | | 0.621*** | | -0.152 | 0.274 |
| I | SJ | 0.053 | -0.074 | | -0.364 | | 0.324 | 0.104 |
| I | SMa1 | 0.117 | 0.181 | | 0.169 | | -0.183 | 0.050 |
| I | SMa2 | **0.254** | **0.269** | | 0.855** | | -0.523*** | 0.410*** |
| I | SMe1 | 0.053 | **0.251** | | -0.010 | | 0.000 | 0.197 |
| I | SMe2 | 0.093 | 0.134 | | 0.443 | | -0.492 | -0.257 |
| II | SF1 | -0.089 | 0.165 | | -0.099 | | -0.834** | -0.460*** |
| II | SF2 | -0.14 | 0.058 | | -0.051 | | -0.529 | -0.130 |
| II | SJ | 0.082 | **0.27** | | -0.394 | | -0.245 | -0.156 |
| II | SMa1 | **0.322** | **0.318** | | 0.275 | | -0.504*** | -0.108 |
| II | SMa2 | **0.249** | **0.243** | | -0.554*** | | 0.330 | -0.309 |
| II | SMe1 | **0.221** | **0.326** | | 0.331 | | -0.765** | -0.155 |
| II | SMe2 | 0.195 | **0.217** | | -0.126 | | -0.124 | -0.151 |
| III | SF1 | -0.011 | **0.316** | 0.017 | | -0.210 | 0.507 | 0.215 |
| III | SF2 | -0.085 | 0.078 | -0.692 | | -0.533*** | -0.204 | 0.502 |
| III | SJ | **0.351** | -0.077 | 0.865*** | | 0.169 | 0.216 | 0.102 |
| III | SMa1 | 0.142 | **0.207** | -0.651** | | -0.393** | 0.168 | 1.067* |
| III | SMa2 | 0.1 | **0.204** | 0.340 | | 0.071 | 0.286 | -0.074 |
| III | SMe1 | **0.311** | **0.486** | 0.054 | | -0.398*** | 0.863** | 0.335 |
| III | SMe2 | **-0.409** | **0.267** | -0.236 | | -0.151 | 0.632*** | 0.260 |

**Table 9**. Estimated factor loadings for common trends in the DFA models with no explanatory variables, as well as factor loadings and regression parameters (with their respective p-values: *<0.05; **<0.01; +++<0.001) in models also with explanatory variables for the three dimensions of trophic space in trophic guild IV. Factor loadings higher than 0.2 are presented in bold font.

| Trophic guild IV | | DFA without explanatory variables | DFA with explanatory variables | | | | |
|---|---|---|---|---|---|---|---|
| | | Trend | Trend | Coefficients (significance) | | | |
| Dimension | Trophic species | Factor Loadings | Factor Loadings | Northern shrimp | BottomTemp | SumGroup4 | Juvenile*Sebastes* |
| I | AD | **0.291** | **0.249** | | | 0.576** | |
| I | AL2 | **0.448** | **0.411** | | | -0.052 | |
| I | AM2 | **0.245** | **0.202** | | | 0.382 | |
| I | GM2 | **-0.298** | **-0.261** | | | -0.587** | |
| I | RH2 | 0.11 | 0.13 | | | -0.541** | |
| II | AD | **0.255** | 0.131 | 0.284 | 0.496*** | | 0.579** |
| II | AL2 | **-0.263** | 0.141 | -0.297 | 0.001 | | -0.326 |
| II | AM2 | **-0.288** | **0.314** | -0.326*** | -0.229 | | 0.224 |
| II | GM2 | -0.05 | -0.005 | 0.099 | 0.483*** | | -0.822** |
| II | RH2 | **0.246** | **-0.299** | -0.077 | 0.744* | | -0.783* |
| III | AD | **0.229** | **0.321** | 0.369*** | | | |
| III | AL2 | **0.248** | **0.301** | -0.097 | | | |
| III | AM2 | **0.323** | **0.388** | 0.356** | | | |
| III | GM2 | **0.245** | **0.25** | -0.323 | | | |
| III | RH2 | 0.163 | 0.187 | 0.131 | | | |

**Table 10**.Prey categories that presented a Pearson Correlation coefficient higher than 0.5 with the time series of each dimension of trophic space for at least 2/3 of trophic species of each guild.

| | **Trophic guild I** | **Trophic guild II** | **Trophic guild III** | **Trophic guild IV** |
|---|---|---|---|---|
| **Dimension 1** | Hyperiidea<br>Northern shrimp | Echinoidea<br>Euphausiacea<br>Hyperiidea<br>Ophiuroidea | Northern shrimp<br>Copepoda | Northern shrimp<br>Hyperiidea |
| **Dimension 2** | Polychaeta<br>Hyperiidea | Ophiuroidea<br>Chaetognata | Chaetognata | Redfish<br>Ophiuroidea<br>Northern shrimp |
| **Dimension 3** | Northern shrimp<br>Hyperiidea | Northern shrimp<br>Ophiuroidea | Northern shrimp | Northern shrimp<br>Redfish<br>Ophiuroidea<br>Hyperiidea<br>Ctenophora |

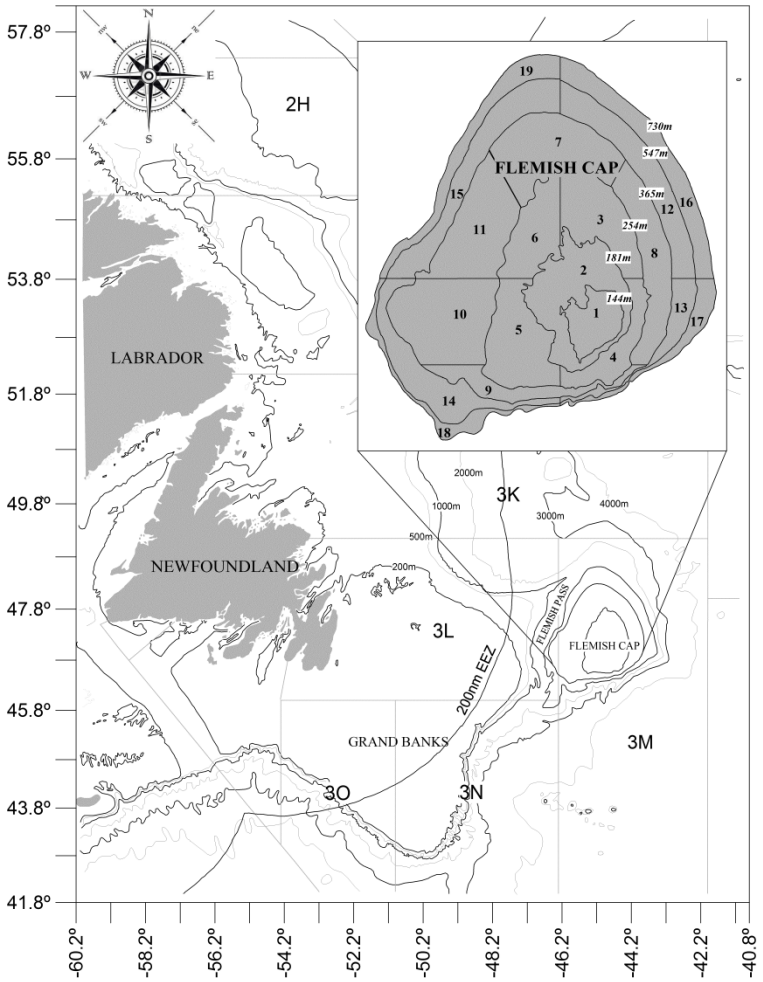


**Figure 1**. The Flemish Cap is located in the 3M NAFO regulatory Division, separated from the Grand Bank by the Flemish Pass, a channel deeper than 1100 m. The inset shows the Flemish Cap area shallower than 730 m with the 19 strata surveyed during the period 1993–2008.

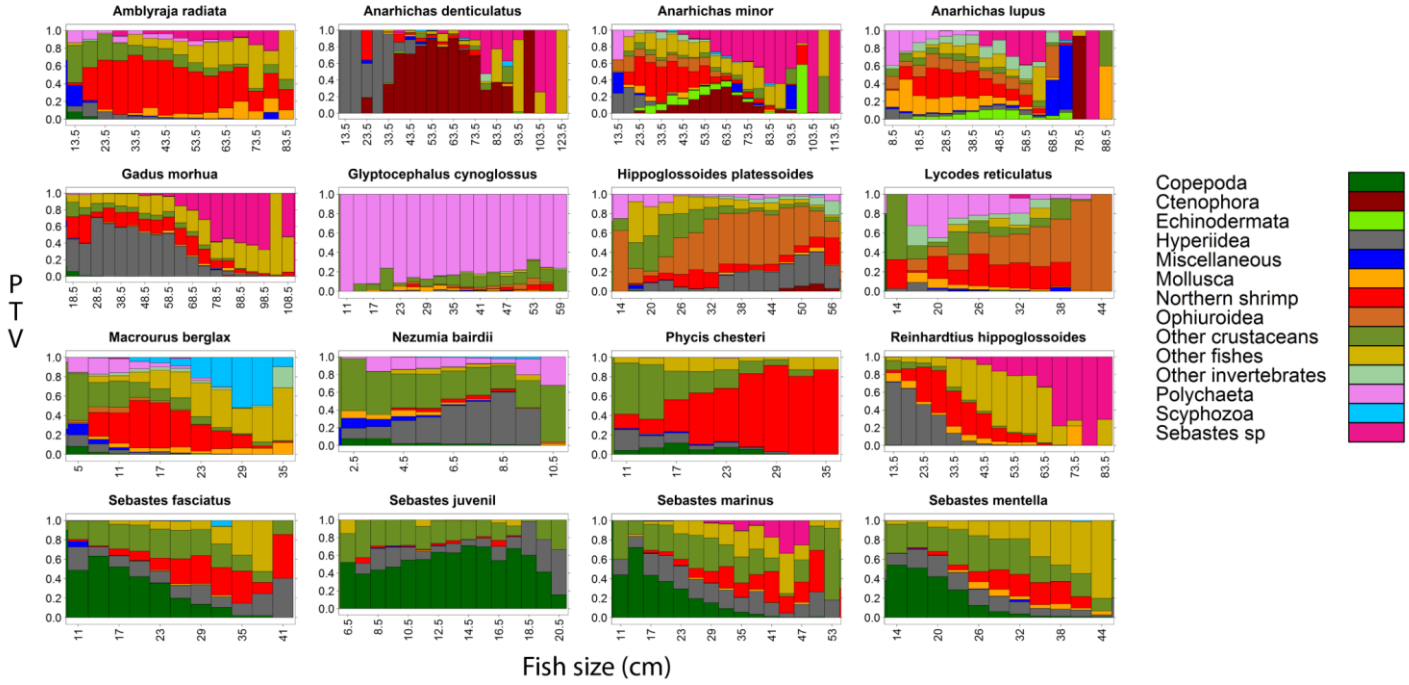


**Figure 2**. Diet composition in percentage over total volume (*PTV*) as a function of fish size for each fish species analyzed in the present work. Although a total of 45 prey categories were used for the analyses described in the text (Table 2), they have been grouped into 14 main prey classes for clarity in the graphical display.

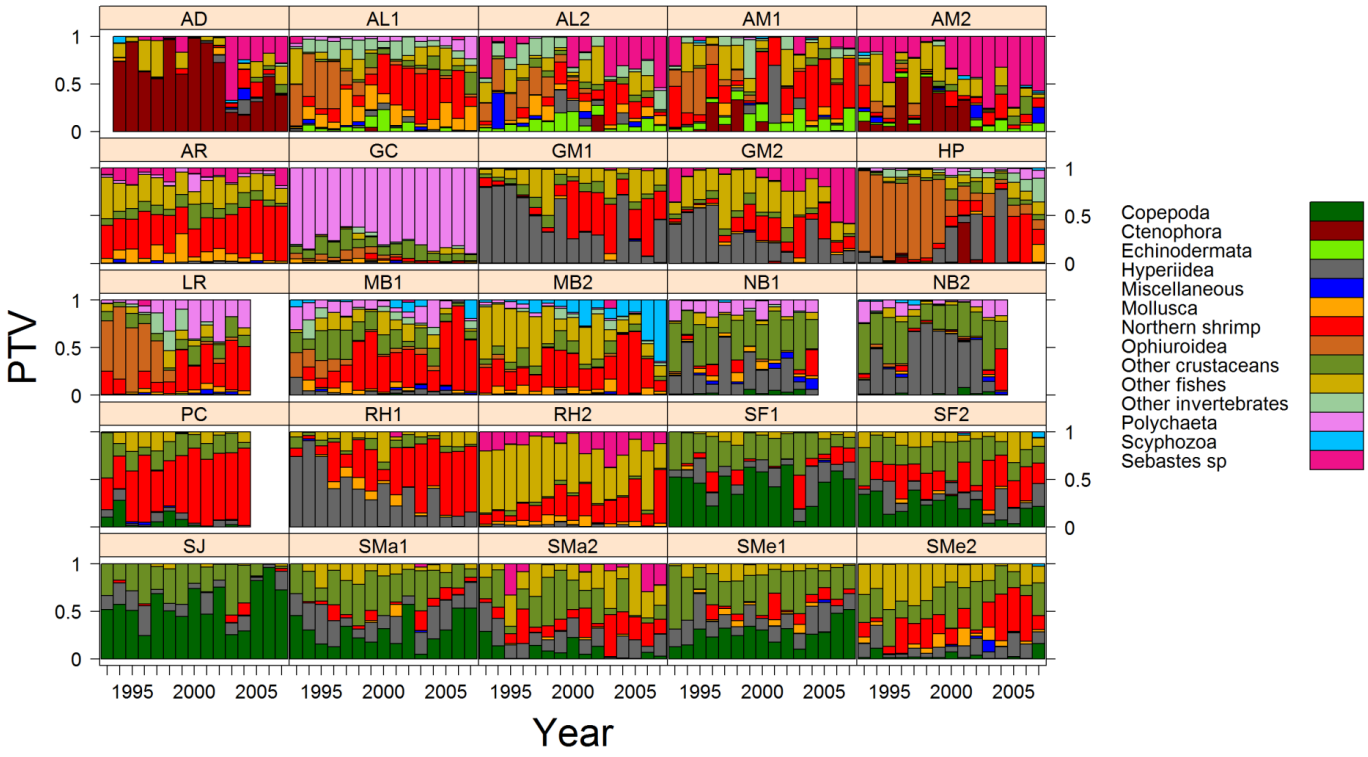


**Figure 3**. Diet composition in percentage over total volume (*PTV*) over time for the trophic species defined in this study (Table 1). Prey categories have been grouped into 14 main prey classes for clarity in the graphical display.

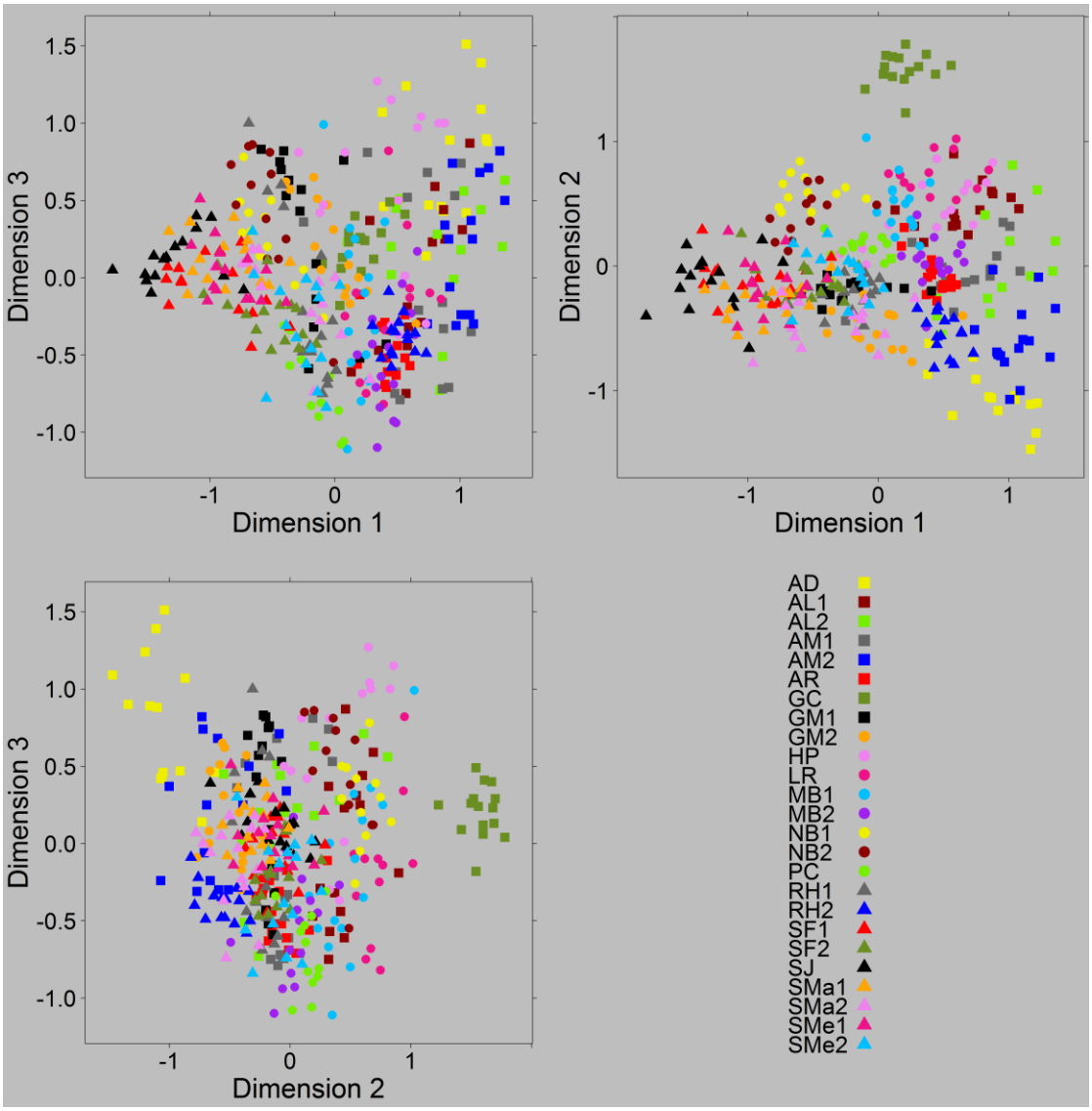


Figure 4.- Distribution of trophic species along the period 1993-2008 on each of the three dimensions of the MDS (i.e. trophic space).

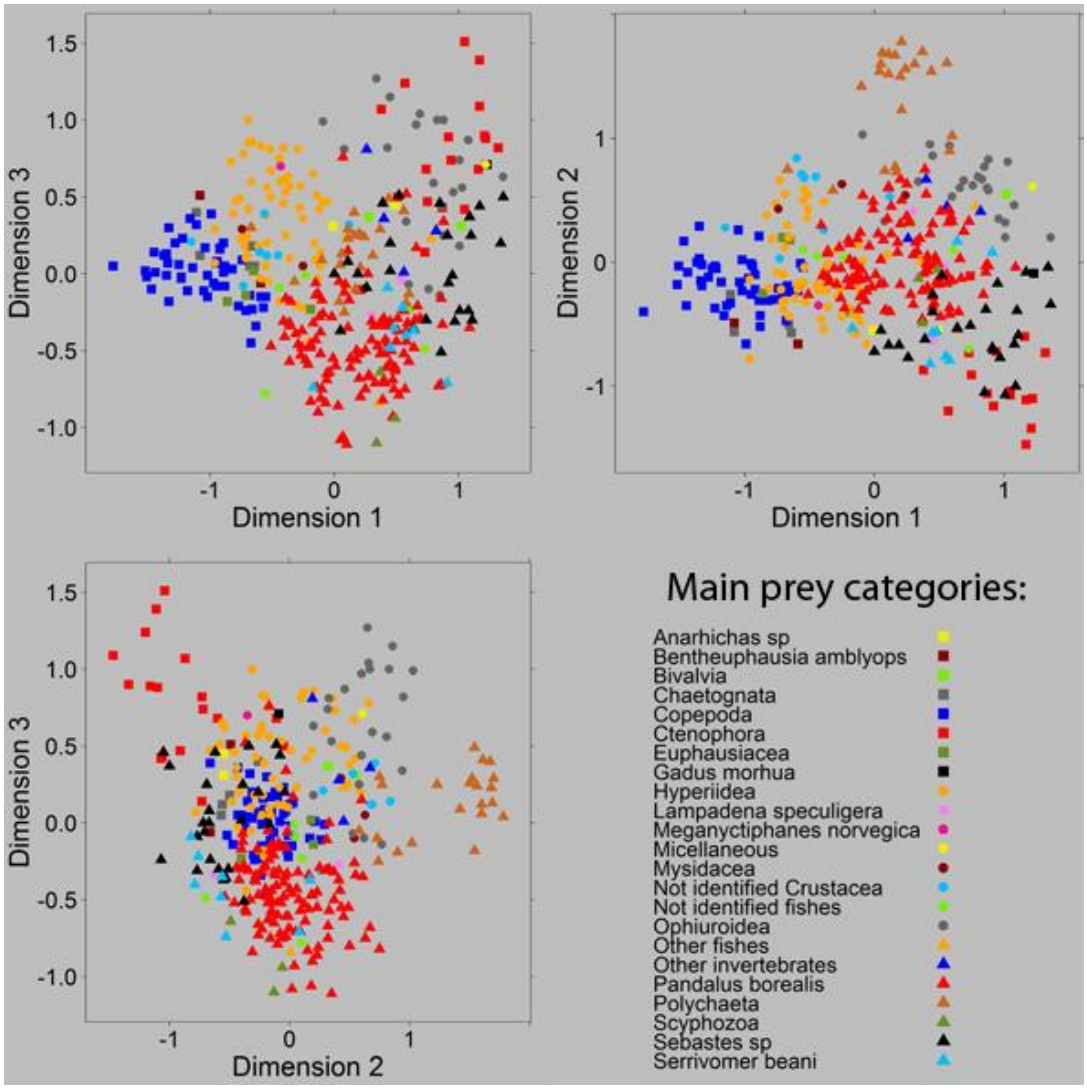


Figure 5.- The category of prey species consumed each year and shown in trophic dimensional space. Prey areas then can be differentiated as those areas where a prey category shows a higher importance over other prey.

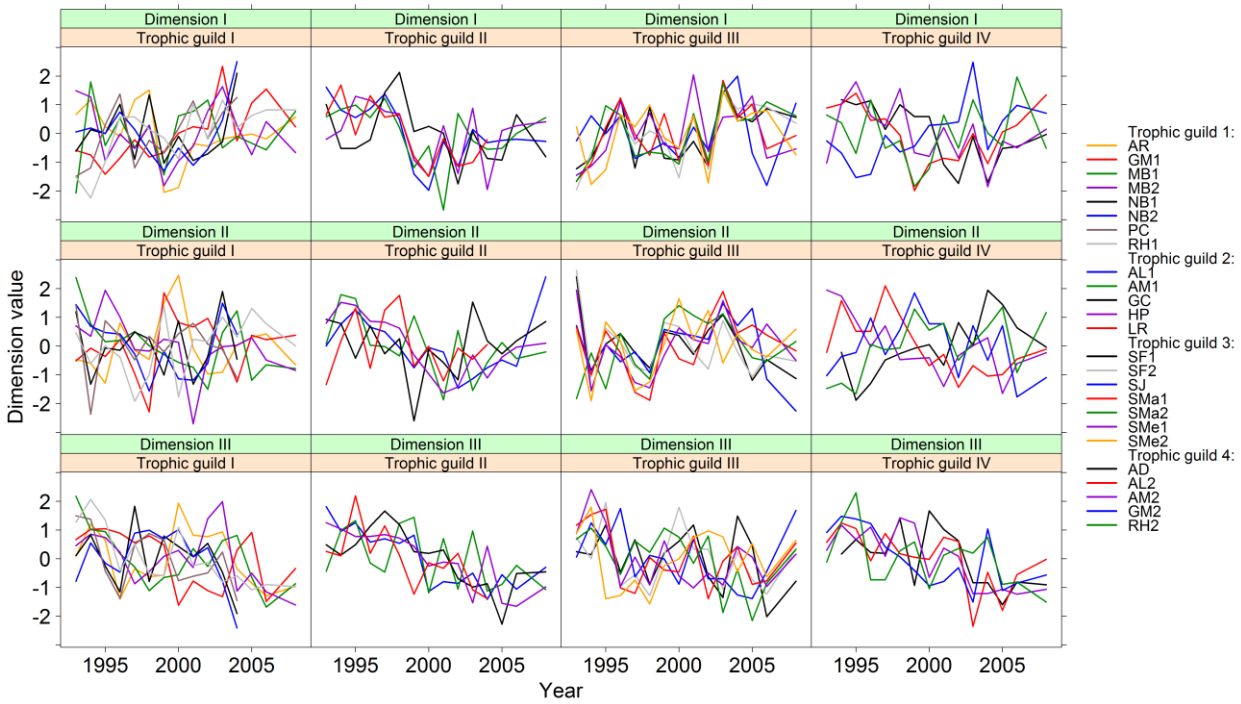


Figure 6.- For each trophic species, normalized values of the three dimensions of the trophic space across the period 1993-2008. Trophic species are grouped into their corresponding trophic guilds.

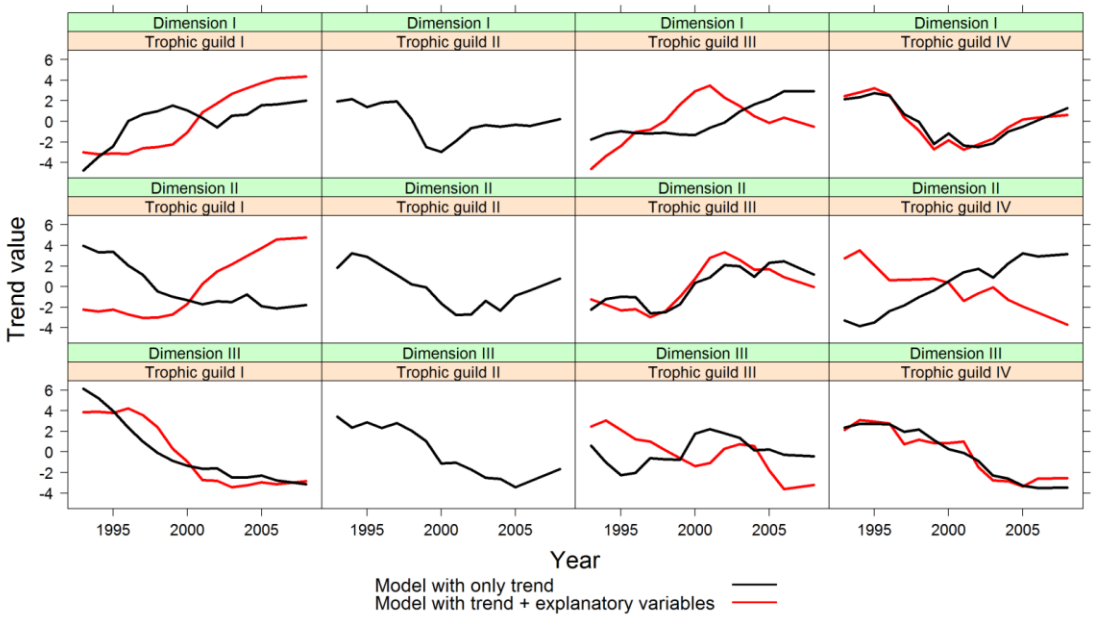


Figure 7.- Common trends from DFA models with and without explanatory variables for each trophic guild and dimension. In trophic guild II only the common trend from the model with no explanatory variables is presented since none of the explanatory variables reduced the AIC in relation to the model including only one common trend.

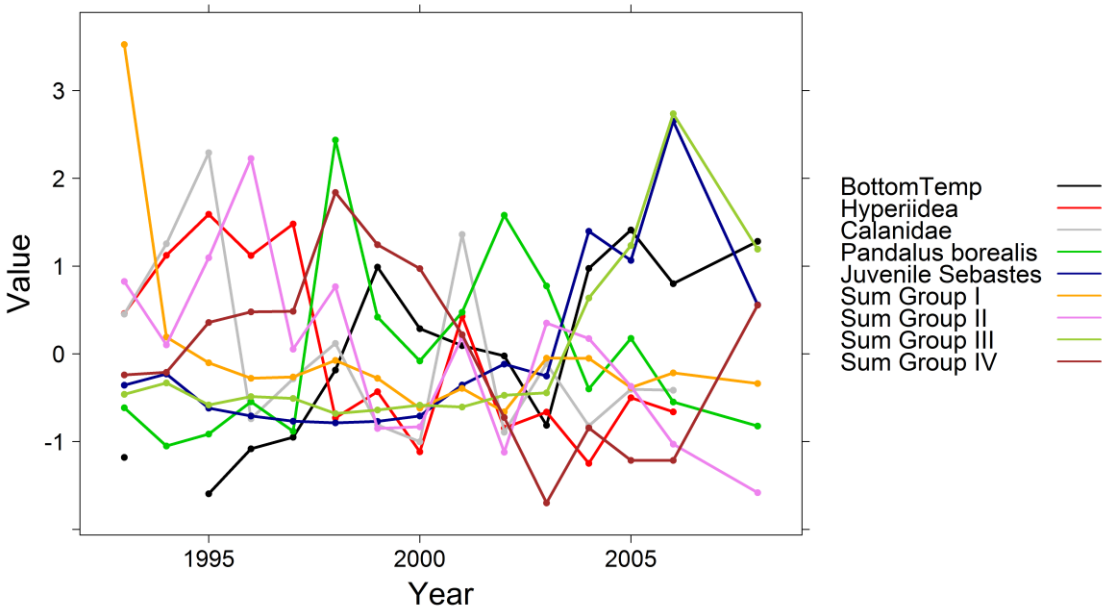


Figure 8.- Normalized values of the explanatory variables used in the fitting process of the DFA models.

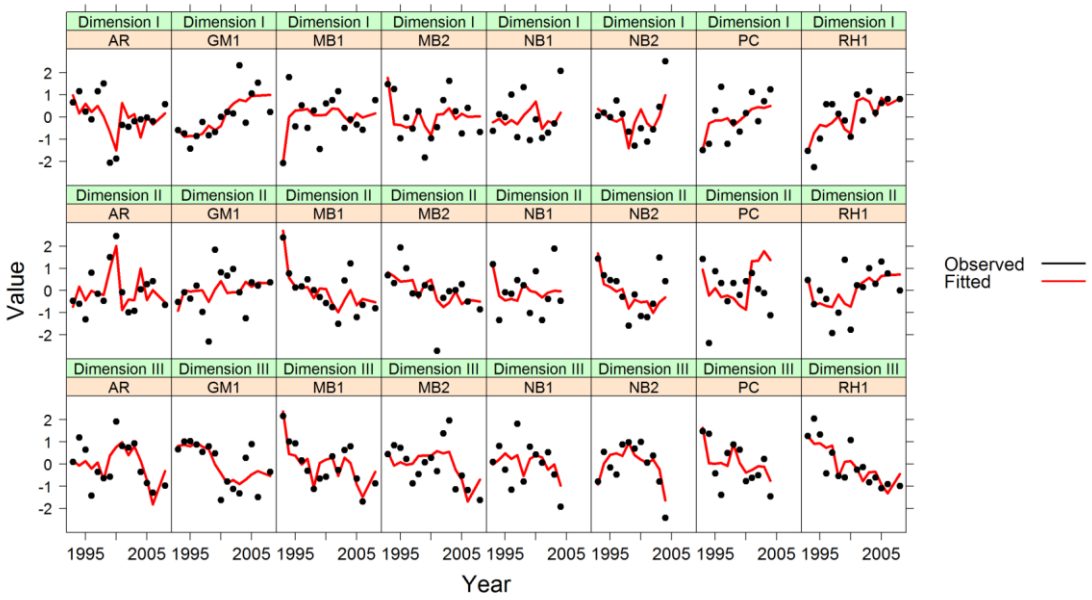


Figure 9.- Observed values for each dimension and trophic species in trophic guild I, and fitted values from the DFA model with the lower AIC.

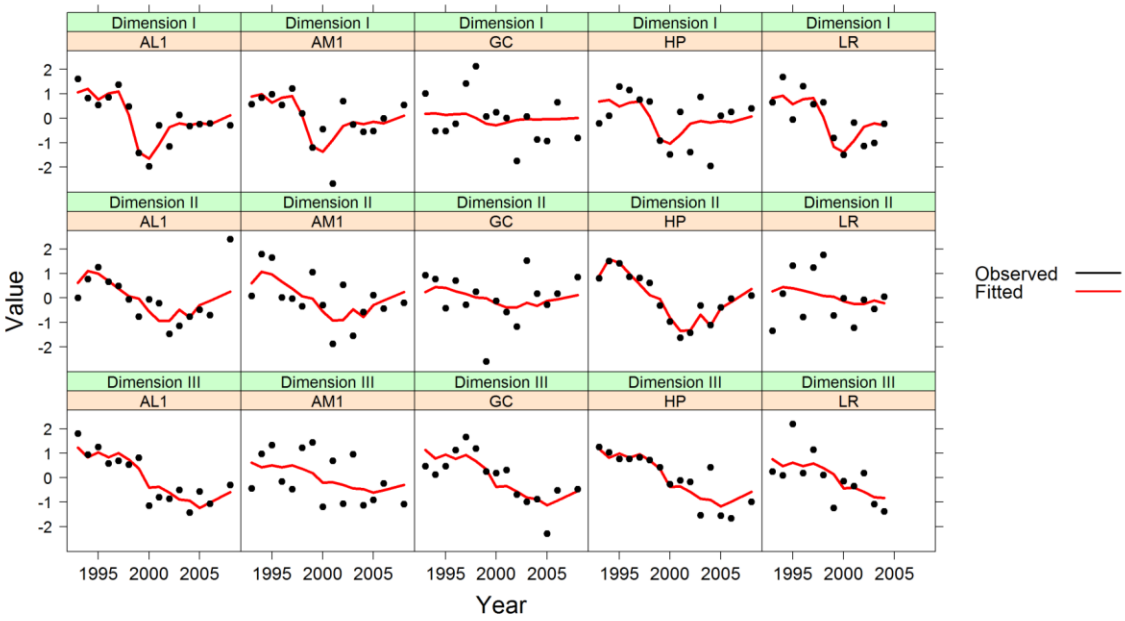


Figure 10.- Observed for each dimension and trophic species in trophic guild II and fitted values from the DFA model with the lower AIC.

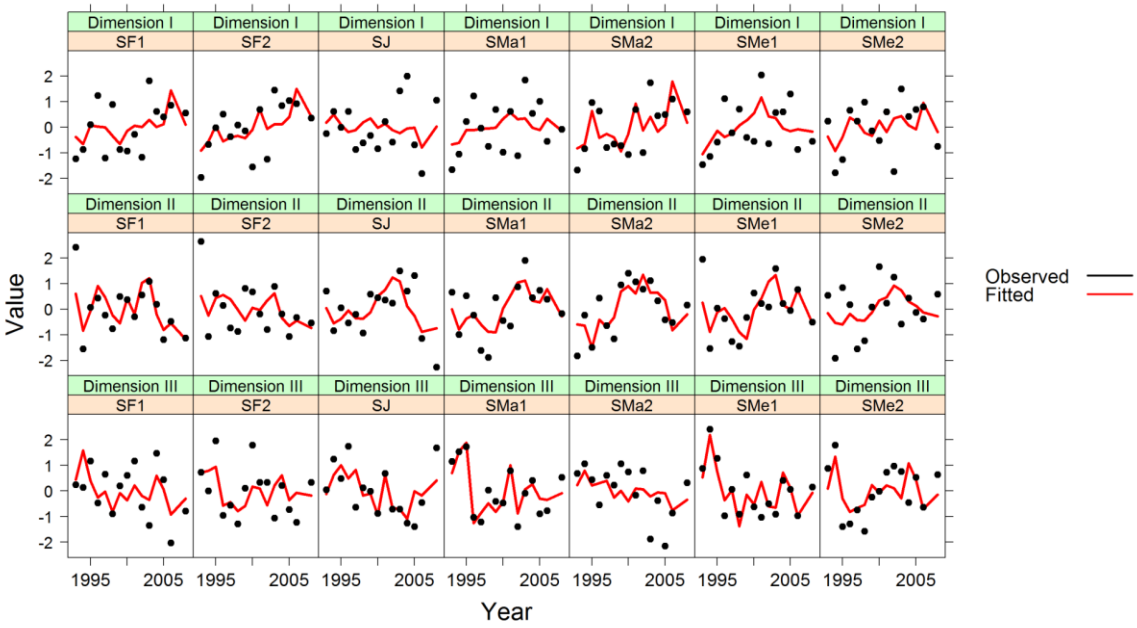


Figure 11.- Observed for each dimension and trophic species in trophic guild III and fitted values from the DFA model with the lower AIC.

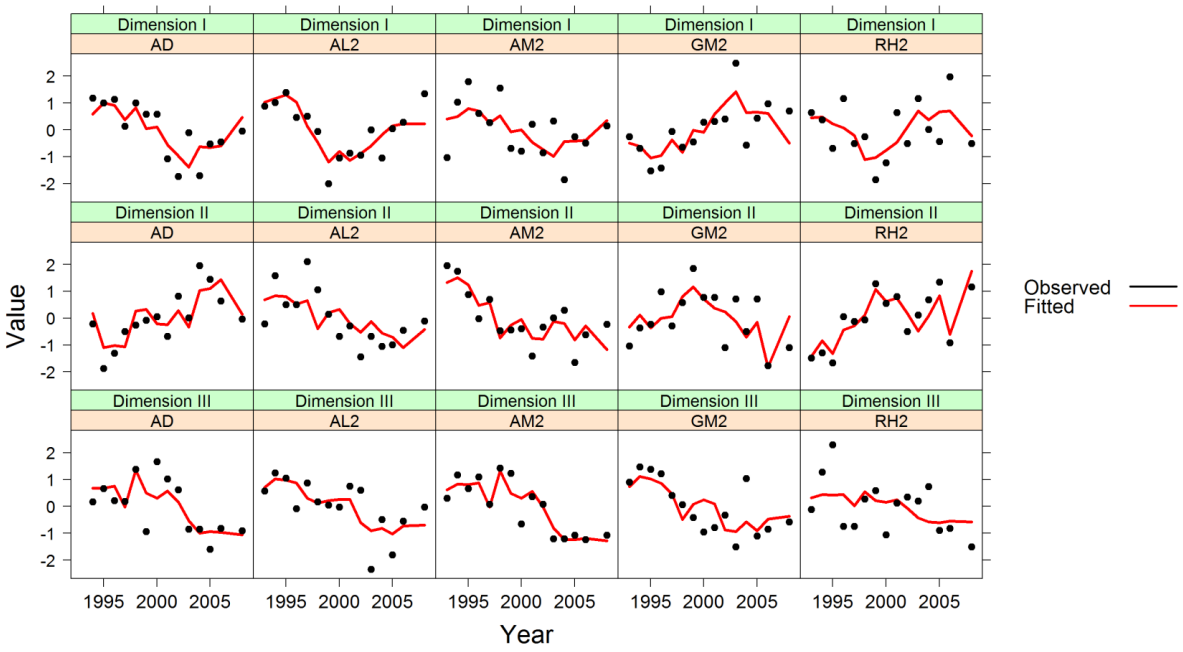


Figure 12.- Observed for each dimension and trophic species in trophic guild IV and fitted values from the DFA model with the lower AIC.

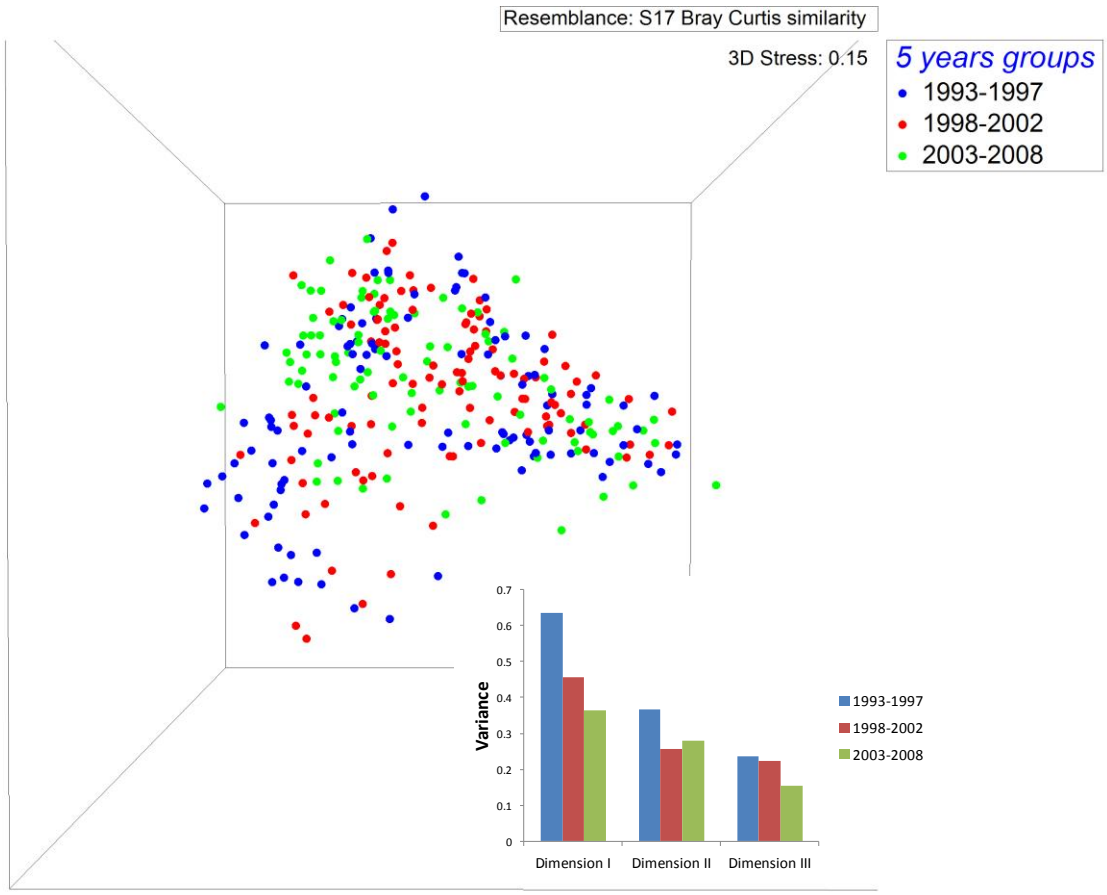


Figure 13.- Data points in trophic space (trophic species-year combinations) have been separated into 3 groups of years: 1993-1997, 1998-2002 and 2003-2008. The estimated total variance on each of the three dimensions is presented in the subpanel for each group of years.